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DISTRIBUTIONAL AND PHYLOGENETIC STUDIES ON INDIAN FOSSIL MAMMALS. II

THE CORRELATION OF THE SIWALIKS OF INDIA AS INFERRED BY THE MIGRATIONS OF *HIPPARION* AND *EQUUS*

BY EDWIN H. COLBERT

INTRODUCTION

Since the first studies of Hugh Falconer and Proby T. Cautley on the Siwalik mammals of India, numerous authors have been interested in the question of the age of the beds in which these mammals were found. A proper knowledge of the age of the Siwalik deposits is essential for a proper understanding of the rich mammalian faunas contained within them, not only because these faunas show successive evolutionary stages in a definitely limited region, but also because these faunas are closely related to other fossil faunas in other sections of Eurasia and North America.

The authors who have been especially concerned with the problem of the correlation of the Siwalik deposits are Hugh Falconer, Richard Lydekker, Guy E. Pilgrim, and W. D. Matthew. As the results of their separate studies of this problem, these students arrived at varying opinions regarding the age of the Siwalik Series, which of course is not surprising, since their collective studies extended over a period of almost one hundred years, and during this time an ever increasing amount of information about Siwalik stratigraphy and Siwalik faunas came to light.

A protracted study of the collection of Siwalik mammals in The American Museum of Natural History has afforded additional evidence bearing on the problem of Siwalik correlation. Therefore it has been thought advisable to publish this paper as an expression of the conclusions reached by the present author regarding the age of the Siwalik Series. The arguments presented below are based not only on the detailed study of the fossils in the American Museum Siwalik collection, but also on observations made in the field by Dr. Barnum Brown, when he was gathering this collection together. The lucid discussions by Dr. Matthew on the question of the correlation of the Siwaliks have been of inestimable value in the preparation of the following remarks.

Comparative Views of Siwalik Correlation

It may be well at this point to consider briefly the several views advocated by the above-mentioned authors as to the correlation of the Siwalik deposits.

Hugh Falconer, the first student of Siwalik mammals, knew only the Upper Siwalik fauna, and this he considered as of Miocene age. Richard Lydekker was acquainted with two Siwalik faunas, namely the Upper one, known to Falconer, and the Middle one. He came to the conclusion that both of these faunas might be placed within the Pliocene period, the Upper Siwalik fauna being of Upper Pliocene age and the Middle Siwalik fauna (designated by Lydekker as the Lower fauna) being of Lower Pliocene age.

The discoveries made by Dr. G. E. Pilgrim first brought the true Lower Siwalik fauna to light. As the result of his studies, especially on the basis of a comparison of Siwalik with Eurasiatic faunas, Dr. Pilgrim came to the conclusion that the Lower Siwalik fauna is of Upper Miocene age, the Middle Siwalik fauna of Lower Pliocene or Pontian age, and the Upper Siwalik fauna of uppermost Pliocene or lowermost Pleistocene age. Working on the lines of different evidence, especially that of the intercontinental migrations of fossil horses, Dr. W. D. Matthew came to somewhat different conclusions from Pilgrim as to the age of the Siwalik faunas. He considered the typical Lower Siwalik fauna to be of Lower Pliocene or Pontian age, the Middle Siwalik fauna to be of post-Pontian age, and the Upper Siwalik, fauna to be of Lower Pleistocene age. My own studies of the several Siwalik faunas substantiates Dr. Matthew's opinion.

A chart, showing the comparative views as to the correlation of the Siwaliks, accompanies this discussion.

The Age of the Lower and Middle Siwaliks as Inferred by the Intercontinental Migration of *Hipparion*

Various lines of evidence tend to make the problem of Siwalik correlation a confusing one, and naturally such a situation has led to differences of opinion among the students of Siwalik faunal successions, as pointed out above. Two methods of attack have been followed in the attempted solution of the perplexing question as to the age of the Siwalik deposits; these are stated below.

1.—The several Siwalik faunas have been studied on the merits of their general aspects, and have accordingly been compared directly with

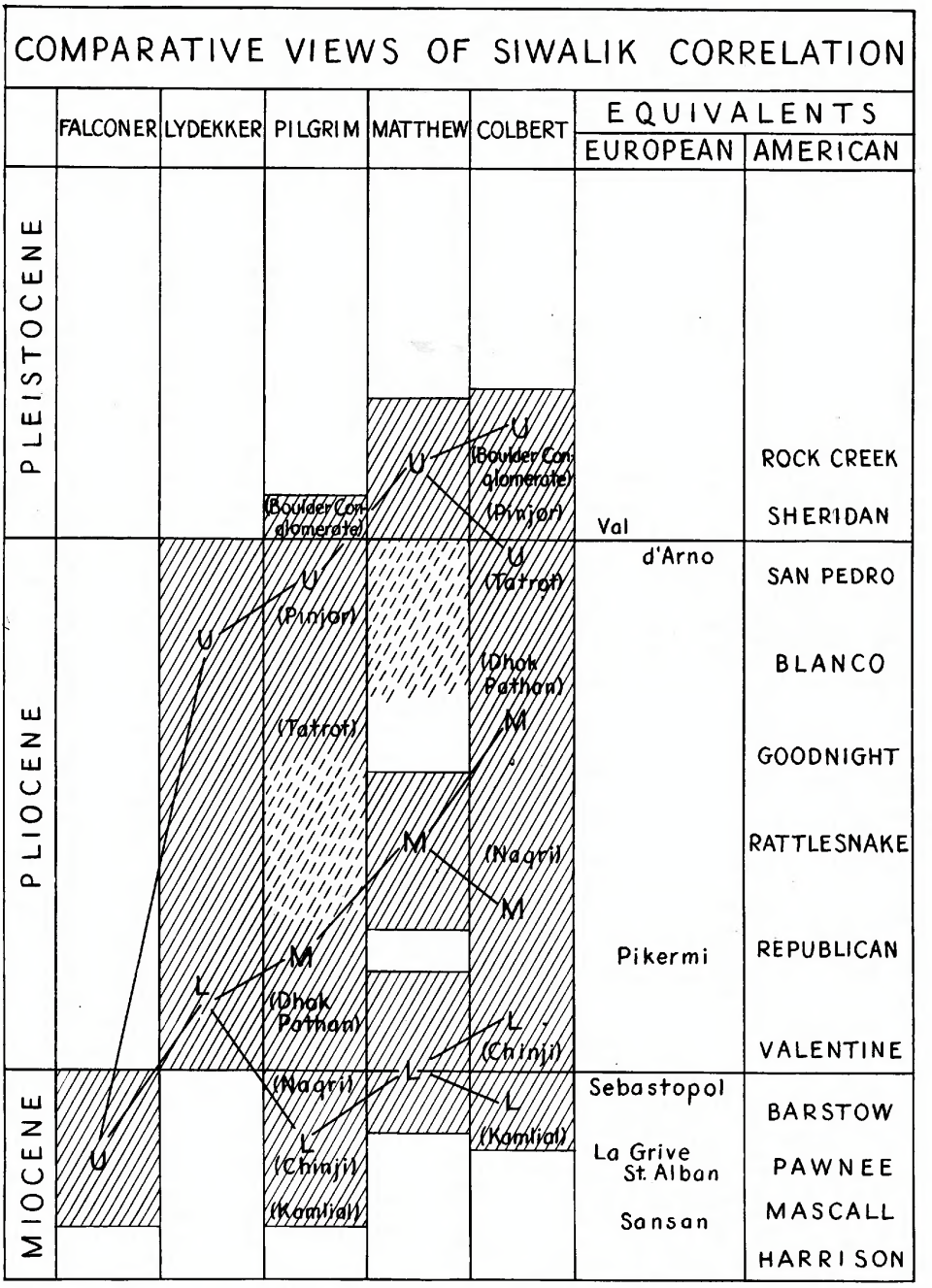

Fig. 1. Comparative views of Siwalik correlation.

the similar faunas of eastern Europe and of Asia. This is the method that has been followed by Dr. Pilgrim.

2.—The Siwalik faunas have been compared not only to the faunas of Europe and Asia, but also to those of North America, and particular attention has been given to the appearances of certain forms invading the Indian region from the North American region. This was the method followed by Dr. Matthew.

Now when the Siwalik faunas are compared directly with similar European or Asiatic faunas, the evidence seems to be greatly in favor of Dr. Pilgrim's views of correlation. The Lower Siwalik fauna is rather distinctly Miocene in its general aspect, for it contains various species of *Dryopithecus*, an hyaenodont (obviously a hold over from earlier times), primitive felids, mastodonts, *Listriodon* and other relatively primitive pigs, a rather primitive anthracothere, *Macrotherium*, and primitive bovids.

In a like manner the typical Middle Siwalik fauna from the Dhok Pathan area shows Pontian affinities. It has Pontian carnivores, *Orycteropus*, closely comparable to *O. gaudryi*, advanced mastodonts, *Hipparion*, *Chilotherium*, *Aceratherium*, rather advanced suids and anthracotheres, cervids, large giraffids, and Pontian bovids. The Upper Siwalik fauna is composed of typical Lower Pleistocene carnivores, mammoths and ungulates. On the grounds of the evidence outlined above, there would seem to be ample justification of Dr. Pilgrim's arguments for the correlation of the Siwaliks.

An examination of the fossil horses, however, throws a somewhat different light on the question.

It is now definitely established, on the basis of the material collected by Dr. Brown, that *Hipparion* is present at the bottom of the Chinji beds, a fact that heretofore has been more or less in question. The importance of this fact will be brought out in the succeeding paragraphs.

The results of many years of exploration and research by various institutions in North America have proven beyond much doubt that the evolutionary history of the Equidae went through all of its major important phases in North America. Moreover, a careful study of the Upper Tertiary Equinae of North America conclusively shows that the genus *Hipparion* has been derived directly from the genus *Merychippus*. There is a gradual and a perfect gradation in the teeth, skulls, and skeletons from the advanced species of *Merychippus*, typical of the Upper Miocene, into the most primitive species of *Hipparion*, typical of the Lower Pliocene of North America.

The characteristic Middle Miocene species of *Merychippus* are medium-sized equines with three toes on each foot, the lateral ones of which do not reach the ground. The upper cheek teeth are rather short-crowned and have square crowns, invested with cement. The enamel borders are relatively simple and the protocone is connected to the protoloph. *Merychippus sejunctus* or *Merychippus isonesus* are typical of the Middle Miocene species of the genus. In the Upper Miocene, a considerable amount of progression is shown over the characteristic Middle Miocene types. The Upper Miocene species, such as *Merychippus republicanus*, are somewhat larger than the older forms, and the teeth are more advanced. The upper cheek teeth are longer crowned, with more complicated enamel foldings, and the protocone tends to be separated from the protoloph in the unworn posterior molars.

Now in the most primitive Lower Pliocene species of *Hipparion* in North America, such as *Hipparion gratum*, a remarkable similarity to the advanced species of *Merychippus* is evident. These primitive forms of *Hipparion* are relatively small, no larger than the advanced *Merychippus*, the cheek teeth are rather short crowned and square, and in the worn molars the protocone is attached to the protoloph, notwithstanding the fact that a separate protocone is a diagnostic character of the genus *Hipparion*. Thus we see that the advanced habitus characters of the progressive species of *Merychippus* become the heritage characters in the primitive species of *Hipparion*. Indeed, the stages of the transition from the one genus into the other are so gradually graded that it is very difficult to draw a distinct line of demarcation between the two.

All of our evidence therefore points to the conclusion that *Hipparion* must have arisen in North America as a direct development from *Merychippus*, subsequently migrating to Asia and Europe. This was the view taken by Matthew, as revealed in the following statement.

"I conclude therefore that the Equinae are surely of American evolution and dispersal and appeared in the Old World as immigrant types."[1]

Now the question arises as to when this migration took place. *Hipparion* first appears in the Valentine formation of North America, which may be regarded either as uppermost Miocene or basal Pliocene. The Valentine forms of *Hipparion*, as particularly exemplified by the species *Hipparion gratum*, are relatively primitive, of small size, with rather simple enamel foldings in the molars, and with the protocone attached to the protoloph in the worn upper cheek teeth.

[1]Matthew, W. D. 1929. 'Critical Observations upon Siwalik Mammals,' Bull. Amer. Mus. Nat. Hist., LVI, p. 529.

On the other hand, the *Hipparion* found at the base of the Chinji beds is a well advanced form, in all respects comparable to *Hipparion theobaldi*, the typical Middle Siwalik species. It has large molar teeth, indicative of a large skull and body, the protocones of the molars are elongated and the enamel foldings of the fossette borders are complex. All in all, the Chinji *Hipparion* is more closely comparable to the American species from the Republican River or equivalent beds than it is to the earlier Valentine forms. This is what we might expect, because there would obviously be a certain time element involved during the migration of the genus from North America to Asia.

Hipparion occurs in Europe, according to Borissiak, at Sebastopol in Sarmatian times. Therefore, if we accept Borissiak's correlation of the Sebastopol deposits, it seems logical to regard the Sarmatian as no older than the Valentine of North America, and probably a little younger. At least, the Sarmatian may be the equivalent of the upper portion of the Valentine. Considering this to be the case, the Pontian would be about equivalent to the Republican River of North America, a view that was advocated by Matthew in 1929.

The base of the Chinji zone, since it contains an advanced *Hipparion*, can be no older than the Sarmatian, and it is very probably equivalent to the upper portion of the Sarmatian or the lower part of the Pontian. But here we meet a difficulty in that the Chinji fauna as a whole is typically more primitive than a Sarmatian or a Pontian fauna should be. The presence of *Hipparion* in the Chinji is, however, incontrovertible evidence against an older age for these beds, so it becomes necessary to regard the Chinji fauna as relict, stratigraphically of upper Sarmatian or lower Pontian age but homotaxially of more primitive affinities. Here we see a striking example of the importance of invading types in determining the age of a fauna. Autochthonous forms may linger on in a certain region, and thus they may be contemporaneous with the advanced invading types, coming into the region from an outside locality. But the invading types furnish the true key to the age of the fauna.

Various European authorities have considered *Hipparion* as of Old World origin, in the face of the very definite evidence to the contrary, outlined above. Of course if *Hipparion* were of Eurasiatic origin, Dr. Pilgrim's views as to the correlation of the Siwaliks would be fully justified. In fact, Pilgrim has considered the possibility not only of an Eurasiatic origin for *Hipparion*, but also the possibility that the genus may have appeared first in the Old World and subsequently in the New World. His views are well expressed in the following remarks, which

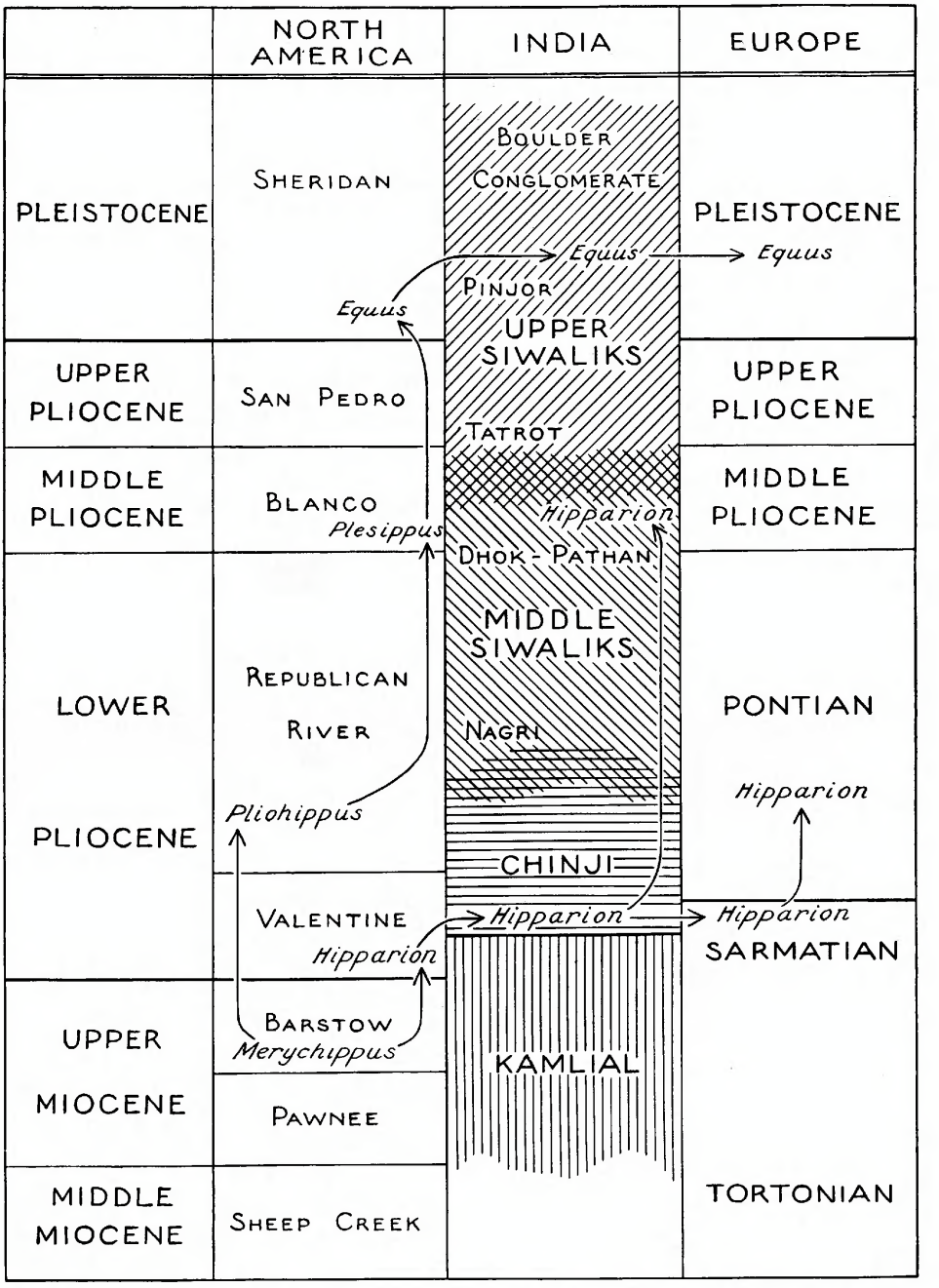

Fig. 2. The correlation of the Siwaliks, as based on the intercontinental migrations of the Upper Tertiary and Quaternary Equidae.

were contained in a private communication to the present author. I take the liberty of reproducing them here.

"The occurrence of *Hipparion* in the Lower Chinji certainly makes it more difficult to correlate that stage with the Tortonian of Europe. But I cannot see how one can disregard the evidence of a whole fauna because one cannot find an explanation of the occurrence of a single form. Questions of migration, character of the fauna, i.e., whether plains or forest enter into the problem of correlation in a way which Matthew himself has rendered abundantly clear. It is a fact that *Hipparion* occurs in Europe in the Sarmatian, and one cannot deny that it is possible that *Hipparion* may have occurred in Central Asia and India even previously to this. I am inclined to think myself that the *Hipparion* of the Old World may be distinct from and have predated the *Hipparion* of America. This has more behind it than mere supposition. The lateral digits of the Old World *Hipparion* are certainly stronger than those of the American *Hipparion*. Where are we to find the links between the earlier American forms and this *Hipparion* with strong lateral digits? Apparently not in America. Whether the lateral digits have been strengthened secondarily, as Matthew thinks, or are a relic of an earlier condition, as I think, does not in the least matter. The point is that somewhere or other the ancestral form of the *Hipparion* of Sebastopol and Pikermi must have existed, and since the American deposits are so well known that its presence could hardly escape notice there, it seems more likely that it will one day be found in the Old World. It may be that the Chinji form might even turn out to be the required link, since we do not know the foot. I cannot even regard it as proved that such a type of *Hipparion* did not live in Tung Gur times. Its absence proves nothing definite, since the fauna is of a forest rather than a plains type, and as such is more likely to have contained *Anchitherium* than *Hipparion*. The rest of the fauna shows nothing, so far as I am aware, which would militate against a Tortonian age, the equivalent of La Grive St. Alban."

The Tung Gur formation referred to by Dr. Pilgrim is an horizon of Upper Miocene age, probably correlative with the Sarmatian of Europe and the Pawnee Creek, Lower Snake Creek and Mascall of North America. See Colbert, E. H., 1934, Amer. Mus. Novitates, No. 690, pp. 5–6.

A reply to Dr. Pilgrim's arguments is presented in the following paragraphs.

As pointed out above, there is a perfect gradation from *Merychippus* into *Hipparion* in North America, and the primitive *Hipparion* of the New World is more primitive than the earliest Eurasiatic species. This

evidence obviates the necessity of supposing a separate origin for the Eurasiatic *Hipparion.*

In the preceding pages an attempt has been made to show that the evidence of a fauna can be outweighed by the evidence of immigrant forms. The Chinji fauna is a primitive persistent assemblage, but the immigrant *Hipparion* defines the age of this fauna.

The strong lateral digits of the Siwalik *Hipparion* do not offer any evidence of a separate origin, as advocated by Dr. Pilgrim. Careful studies of the material in the American Museum collection have shown that the lateral digits in the Siwalik *Hipparion* are strong because the entire foot is robust and heavy. Considered from the standpoint of relative proportions, the lateral digits of the Siwalik *Hipparion* are really not any more developed than the lateral digits in the small, slender species of North American *Hipparion.*

But even if this were not the case, even if the lateral digits were actually proportionately larger in the Siwalik *Hipparion* than they are in the North American *Hipparion,* Dr. Pilgrim's argument would not necessarily be substantiated. We know that reversals in evolution are not at all uncommon in the phylogenetic development of various groups of mammals. To argue that reversals in the development of the lateral digits of the Equinae could not have occurred, that there would not have been secondary enlargements of the side toes, is to argue against a phenomenon for which we have abundant evidence. It is giving undue weight to the processes of orthogenesis.

(The details concerning the development of the lateral digits in the Siwalik *Hipparion,* as contrasted with the North American *Hipparion,* are presented in a forthcoming memoir, dealing with the American Museum Siwalik collection.)

As to the argument that the American deposits are so well known that an ancestor of the Pikermi *Hipparion* could "hardly escape notice there," this line of reasoning may be reversed with equal facility. Certainly the European deposits are pretty well known, as are the Asiatic (due to the work of the Swedish and the American expeditions during the past fifteen years), and if an ancestor of *Hipparion* were to be found in them it should have probably turned up by this time. As a matter of fact, there is no equine in the European or the Asiatic Tertiary that is ancestral to *Hipparion,* and since such parental forms are to be found perfectly exemplified in the advanced species of *Merychippus* in North America, it seems only reasonable, at least on the basis of our present knowledge, to suggest that the origin of the genus *Hipparion* was in the New World.

Nor can the Chinji *Hipparion* be a primitive link, as Dr. Pilgrim suggests, because it is fully as advanced in structure as the later Middle Siwalik *Hipparion*.

In the light of these considerations, there seems to be but one course to take, and that has been indicated above.

1.—*Hipparion* is of North American origin, descended from *Merychippus*.

2.—It migrated to Eurasia.

3.—It arrived in Eurasia subsequent to its appearance in the Valentine (basal Pliocene) of North America.

The foregoing arguments have been concerned chiefly with the problem of the Chinji fauna and its age. It has been shown that the Chinji fauna is equivalent to or later than the Valentine fauna of North

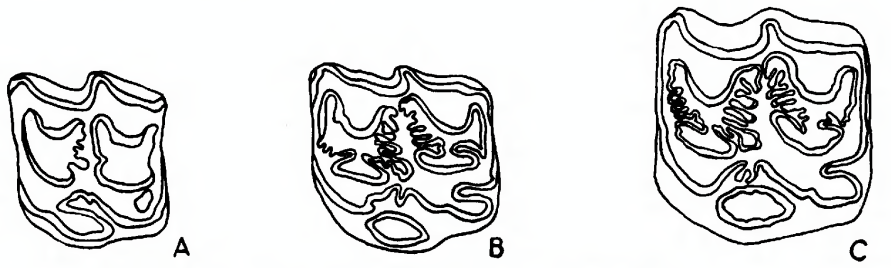

Fig. 3. *Hipparion* molars from North America and India.

A. *Hipparion gratum*, Valentine, Lower Pliocene, North America.

B. *Hipparion mohavense*, Ricardo, Lower Pliocene, North America.

C. *Hipparion theobaldi*, Chinji, Lower Pliocene, India.

A and B from Osborn, 1918. All figures natural size.

This chart illustrates the rapid structural evolution of the *Hipparion* molar during Lower Pliocene times.

America, which would make it either of uppermost Sarmatian or of Pontian age.

Coming now to the typical Middle Siwalik fauna, we find that it is separated by an appreciable time interval (as represented by a considerable thickness of continental sediments) from the Lower Siwalik or Chinji fauna. Therefore the Middle Siwalik fauna must be of post-Upper Sarmatian or post-Pontian age, and the probabilities are in favor of the latter consideration. But, since the Middle Siwalik fauna is homotaxially of Pontian affinities, we must consider the probability of its having persisted on into post-Pontian times with little changes among the forms that constitute it. Thus the Middle Siwalik fauna has followed the same trend of persistence that characterized the Chinji fauna.

The Age of the Upper Siwaliks as Inferred by the Intercontinental Migration of *Equus*

Discoveries made during the course of the past ten years prove beyond much doubt that the genus *Equus* is of North American origin. It is to be derived from the genus *Plesippus*, described by Matthew, which in turn is descended from *Pliohippus*. *Hipparion*, often cited by European authorities as a form ancestral to *Equus* is in reality a phylogenetic side line that eventually became extinct without giving rise to any later forms.

Just as a continuous series of gradations connect *Merychippus* and *Hipparion*, so does *Merychippus* evolve into *Pliohippus*. The change from the earlier to the later form in this case is marked by:

1.—An increase in size.

2.—An increase in the length of the limbs.

3.—A reduction of the lateral digits, and a complete suppression of the phalanges on the lateral digits, in most species.

4.—An increase in the size and hypsodonty of the cheek teeth.

5.—Retention of the simple enamel foldings on the fossette borders of the upper cheek teeth.

6.—Retention of a connection between the protocone and the protoloph of the upper cheek teeth.

An evaluation of the above listed structural changes demonstrates a trend in the direction of *Equus*. Points three, five, and six are especially significant. In *Hipparion* the lateral digits are well developed, the enamel of the upper cheek teeth becomes complexly folded and the protocone becomes isolated from the protoloph. These are characters that mark the aberrant position, if we wish to call it that, occupied by *Hipparion* in the phylogenetic scheme of the Equidae. Now in these particulars *Pliohippus* does show a definite trend towards the *Equus* condition and this trend is still further developed in the genus *Plesippus*.

Plesippus is a large horse, as large as the wild species of *Equus*, in which the lateral digits are reduced to mere splints. The skull and teeth are very close to the skull and teeth of *Equus*, but they show certain *Pliohippus* characters. *Plesippus* forms a perfect link between *Pliohippus* and *Equus*.

Therefore it seems well proved that *Equus* had its origin in North America, and that it subsequently migrated to Eurasia.

The first appearance of *Equus* in North American deposits is at the base of the Pleistocene. Following the same line of reasoning that applied to *Hipparion*, it at once becomes evident that the first appear-

ance of *Equus* in Eurasia must be subsequent to its appearance in America. Therefore *Equus* must mark the Pleistocene in the Old World, and the appearance of this genus in the Upper Siwalik deposits denotes the Pleistocene age of these beds.

Concluding Remarks

Should the evidence of one or two genera, namely *Hipparion* and *Equus*, be given weight over the evidence of entire faunas in deciding questions of correlation? In the case of the Siwalik problem, it should, because the horses in the Siwaliks are the invading elements from North America, while the large portion of the other animals in the several faunas are indigenous in their origin. Dr. Matthew has advocated the importance of invading forms in a fauna; he has shown that new forms suddenly appearing from outside in an assemblage of animals are much safer guides as to the age of the assemblage than are the indigenous members alone. Animals that have evolved in a certain region may persist on past the period of their typical expression, thereby extending the time range of their faunal association and thus introducing doubts as to their true age, but as to the appearance of invading forms there can be little doubt. Invading animals link up a fauna with other definitely known faunas, thereby giving clues to the true correlation of the assemblage. For these reasons the arguments set forth in the foregoing pages are considered as giving the valid evidence regarding the correlation of the Siwalik deposits of India.

Additional Remarks

Since the foregoing remarks were written, a paper by Teilhard and Stirton[1] has appeared, which has some bearing on the problem of the correlation of the Siwaliks. In the above-mentioned paper (correlation table, p. 284) the Lower Siwaliks are indicated as of uppermost Vindobonian age, the Middle Siwaliks are correlated with the Pontian, and the Upper Siwaliks are placed in the Astian, or uppermost Pliocene. This correlation, though in a way somewhat intermediate between Pilgrim's and Matthew's correlations, does tend to favor Pilgrim's views as to the age of the Siwaliks.

On pages 281 and 282 of the above-cited work the following statement appears.

[1]Teilhard de Chardin, P., and Stirton, R. A. 1934. 'A Correlation of some Miocene and Pliocene Mammalian Assemblages in North America and Asia with a Discussion of the Mio-Pliocene Boundary.' Univ. of Calif. Publ., Bull. Dept. Geol. Sci., XXIII, No. 8, pp. 277–290.

"The argument has been advanced that, because *Hipparion* is derived from the North American Miocene genus *Merychippus*, hipparions should appear in North America in the Upper Miocene or prior to their appearance in Europe. There is good evidence, however, which indicates that *Neohipparion* and *Nannippus* are derived from different species of *Merychippus;* accordingly, the Old World hipparions are probably descendants of an unknown Asiatic *Merychippus* or a *Merychippus* in this country older than the Niobrara River fauna, which contains advanced species of *Merychippus* showing intergradation with *Neohipparion* and *Pliohippus*. At least, the species of *Merychippus* which show intergradation with the American genera did not give rise to *Hipparion* of the Old World."

The Niobrara River fauna, referred to in the foregoing quotation, is equivalent to the Valentine fauna contained in the Valentine formation, as used by Matthew, Simpson and others.

If the Old World *Hipparion* was independently derived from an Asiatic species of *Merychippus*, the arguments set forth in the earlier pages of this present paper are materially weakened, and Pilgrim's views as to the correlation of the Lower and the Middle Siwaliks are strengthened. On the other hand, there is no real evidence for supposing that the Old World *Hipparion* was derived from an Old World *Merychippus*. In the first place, an Old World *Merychippus* has never been found. Pilgrim speaks of some of the Chinji *Hipparion* as being "slightly smaller and more brachyodont" than the Middle Siwalik *Hipparion*. The material in the American Museum collection indicates, however, that the Chinji *Hipparion* was but little different if at all separate from the Middle Siwalik *Hipparion*. Thus, neither an Old World *Merychippus* nor a primitive Old World *Hipparion* is known from the material extant.

In the second place, it seems rather unnecessary to postulate an Old World *Merychippus* or a primitive Old World *Hipparion* as the ancestors of the typical Old World *Hipparion*, since perfectly good structural ancestors of the proper kind are to be found in North America. *Hipparion gratum*, *Hipparion gratum tehonense* and related species would seem to be adequate as ancestral types for the Old World *Hipparion*. These species have, as do the Old World forms, a round oval protocone, a moderately high molar crown, a rather deep lacrymal fossa, and other features in common. Moreover, the North American form is primitive, as we might expect an ancestral species to be.

In Teilhard and Stirton there is a statement to the effect that the

"species of *Merychippus* which show intergradation with the American genera [of *Hipparion*] did not give rise to *Hipparion* of the Old World." This may be true, but it does not argue against the strong probability that *Hipparion gratum* and its related species are the direct ancestors of the Old World *Hipparion*. Moreover, the primitive characters of *Hipparion gratum* as contrasted with the advanced and specialized characters of all of the Old World members of the genus, even the earliest forms, show that a certain time element was involved in the migration of the genus from North America to Eurasia.

Since there is no definite proof for the separate origin of the Old World *Hipparion* in Eurasia, it seems reasonable to look for their ancestors in North America, typified by such species as *Hipparion gratum*. Since even the earliest of the Eurasiatic *Hipparion* are relatively advanced and specialized species, it is reasonable to think that a certain amount of geologic time passed between the appearance of the genus in North America and its migration to Asia and Europe. Therefore the correlation of the Siwaliks as advocated by Matthew and as reviewed in the preceding pages of this paper would seem to be justified on the basis of all of the available evidence now known.

In the paper by Teilhard and Stirton the Valentine formation of northwestern Nebraska is divided. The lower phases supposedly transitional between the Miocene and the Pliocene are named the Niobrara River, whereas the upper portion, said to be transitional between the Lower and the Middle Pliocene, retains the name Valentine. The name Valentine is well established in the literature to indicate the formation and the time transitional between the Miocene and the Pliocene, and the abandonment of this usage of the term will lead to some confusion. Lacking more detailed and conclusive evidence on the question of the proposed division, the name Valentine, indicative of the transition from the Miocene to the Pliocene, is retained in the foregoing pages in its original meaning.

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